Coexistence of Hydroid Eating Nudibranchs:
Do Feeding Biology and Habitat Use Matter?

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Abstract. The feeding biologies and habitats of four nudibranchs in colonies of the hydroid *Obelia geniculata* were investigated to determine whether these factors contribute to the coexistence of the nudibranchs. The radulae and feeding behaviors showed species-specific traits. *Dendronotus frondosus* has a multi-seriate radula; when small (<5 mm), individuals are suctorial feeders, whereas larger nudibranchs (>5 mm), bite whole polyps. *Doto coronata* uses a flat, uniseriate radula to penetrate stolons. *Eubranchus exiguus* penetrates hydrothecae with a triseriate radula. *Tergipes tergipes* has a curved, uniseriate radula and rakes naked tissue.

Each species of nudibranch occupied a distinct area within the hydroid colony, suggesting that the micro-habitats are dictated by feeding biology. *D. frondosus* occupies hydrocauli towards the center of the colony, *D. coronata* occurs along the edge of the colony on the kelp surface, *E. exiguus* is found on hydrocauli at the edge of the colony, and *T. tergipes* sits atop tall hydrocauli in the center of the colony.

Separation in the hydroid food resource exists among these nudibranchs and equilibrial coexistence could have operated, but equilibrial conditions necessary for exclusion are unlikely to occur or persist significantly long. Thus, this assemblage of nudibranchs appears structured by non-equilibrial processes perhaps similar to populations of phytophagous insects.

Introduction

In aquatic environments, the coexistence of sessile species has received much attention (Osman, 1978; Jackson, 1984; Keough, 1984; McGuinness and Underwood, 1986; Ojeda and Dearborn, 1989) where most studies are ex-

amples of pre-emptive or overgrowth competition of clonal invertebrates (Schoener, 1983). The co-occurrence of motile invertebrates in epifaunal and algal communities is well documented (Edgar, 1983; Coyer, 1984; Virnstein and Howard, 1987; Hall and Bell, 1988), but the mechanisms allowing their coexistence are generally unknown (Seed, 1986). Although variability in diet (Nybakken and Eastman, 1977; Shonman and Nybakken, 1978; Fernandez *et al.*, 1988), radular structure (Bloom, 1976; Blinn *et al.*, 1989), feeding behavior (Hawkins *et al.*, 1989), habitat preference (Bloom, 1981) and temporal appearance on the food resource (Yoshioka, 1986) provides explanations for the coexistence of epifaunal gastropod predators, little is known of the relationship of co-occurring nudibranchs in hydroid colonies (Todd, 1981).

The majority of nudibranchs in the Gulf of Maine prey on hydroids (Meyer, 1971; Clark, 1975; Lambert, 1985). Often nudibranchs demonstrate considerable overlap in their distribution with many nudibranch species feeding in the same hydroid colony (Kuzirian, 1979). Coexistence in these hydroid colonies may be mediated by differences in habitat or food, but the underlying mechanisms are unknown.

The hydroid *Obelia geniculata* grows epiphytically on laminarian kelps, often covering the entire blade surface. Four species of nudibranchs (*Dendronotus frondosus*, *Doto coronata*, *Eubranchus exiguus*, and *Tergipes tergipes*) inhabit these colonies sympatrically. Their spatial distribution within the colony suggests a separation in their use of the hydroid as food and micro-habitat. This study focuses on the feeding biology and micro-habitat use of those nudibranchs inhabiting colonies of *O. geniculata*. For each nudibranch species the following parameters are described: morphology of the radula, feeding behavior, and location within the hydroid colony. Skeletal morphology of the hydroid prey is also described. Differences

in trophic morphology and feeding mechanisms among predators may reflect the diets of these predators within hydroid colonies. The possibility that differences in feeding biology and habitat use help facilitate coexistence among these nudibranchs is considered.

Materials and Methods

Collection of animals

Nudibranchs and colonies of *Obelia geniculata* were collected from a shallow (4–10 m), kelp bed at Cape Neddick, York, Maine, (43° 10′ N, 70° 36′ W) from September, 1988, to September, 1989. Kelp blades (*Laminaria saccharina* and *L. digitata*) were examined underwater for nudibranchs, individually placed in plastic bags, and brought to the lab. In the lab, four species of nudibranchs (*Dendronotus frondosus*, *Doto coronata*, *Eubranchus exiguus*, and *Tergipes tergipes*) were isolated from the hydroid colonies, sized to the nearest mm with a dissecting microscope, and separated for different parts of the study.

Analysis of radulae

Radulae from four individuals each of *D. frondosus*, *D. coronata*, and *E. exiguus* and seven individuals of *T. tergipes* were examined. Entire animals were dissolved in 10% NaOH for 10–12 h. The radulae were then teased free and placed into 70% ethanol until they were mounted for scanning electron microscopy (SEM). Clean radulae were mounted onto glass coverslips in a drop of distilled water and allowed to air-dry. They were sputter coated with a 200–300 Å coating of Au/Pd and viewed with an AMR 1000 Scanning Electron Microscope at 20 kV.

Six parameters from three tooth rows from the center of each radula were quantified for each species; the aim was to characterize the morphology of the radula from each nudibranch species. From a dorsal perspective, the width (μm) of the radula and the length (μm) and width (μm) of the rachidian tooth were measured and the denticles on one side of the rachidian tooth were counted (Fig. 1A). The rake angle and curvature of the radula were measured from a lateral view (Fig. 1B). The rake angle (defined as the angle of the radula to the feeding surface when protruded from the mouth) was measured as the angle made from the tip of the rachidian tooth to the base of the tooth row. Curvature is the degree of hook or the amount of concavity along the inner margin of the radula (Bloom, 1976). Curvature was measured as the ratio between the height of the concavity along the inner margin of the rachidian tooth and the length of the rachidian tooth. All length measurements and angles were obtained from the SEM photos with a digitizing tablet.

A multivariate analysis of variance (MANOVA) was used to test the null hypothesis that no morphological
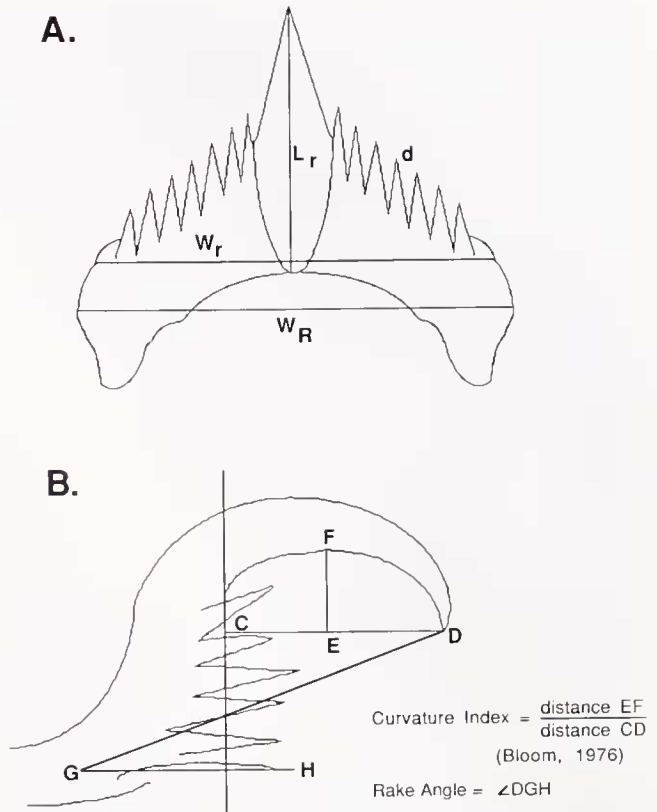

Figure 1. Drawings of a radula tooth from a (A.) dorsal and (B.) lateral perspective. Schematics show the measurements made to quantify radular structure. (W_R = width of radula, W_r = width of rachidian tooth, L_r = length of rachidian tooth, d = denticles.)

differences in radular structure existed among the nudibranchs (Harris, 1985). Data were ln (x + 1) and square root (x + 0.5) transformed to correct for non-normality and heteroscedastic variances (Zar, 1984).

Feeding behavior and feeding damage

Feeding mechanisms were identified for each species of nudibranch. Nudibranchs were starved overnight and were then placed in 10 cm (diameter) stacking dishes containing kelp blades covered with *O. geniculata*. The feeding behaviors of each nudibranch were observed with a stereo microscope during a minimum of six feeding sessions. A feeding session consisted of approach, attack, manipulation, and consumption of the hydroid prey, and a session was considered complete when the nudibranch retreated from the polyp or stolon it had been eating.

Portions of hydroids that had been manipulated were collected from the colony as the nudibranchs were feeding. Where possible, the pieces of stolon were cut 0.5 cm from a site of feeding and lifted from the kelp surface. If the

stolon could not be easily removed, the kelp itself was cut so that the feeding area could be obtained. Uprights were also removed from the colony after having been fed upon by nudibranchs. Hydroid skeletal pieces that had been fed upon were taken from each nudibranch species except *T. tergipes*, which feeds on naked tissue. All hydroid pieces were preserved in 2.5% phosphate buffered glutaraldehyde for 1–2 h and then stored in 70% ethanol. For SEM, the tissues were dehydrated through a graded ethanol series and placed in hexamethyldisilizane (HMDS) for final drying (Nation, 1983). Skeletons were mounted on stainless steel stubs with double-stick tape and coated as described for the radulae. The dimensions of the holes produced by the nudibranchs were measured on SEM photos with a digitizing tablet.

Nudibranch habitats

Hydroids with their nudibranchs were placed in flowing seawater and examined within 24 h. The location of each nudibranch within its colony was determined and quantified by four habitat parameters: (a) height of the nudibranch above the kelp surface (mm), (b) density of hydrocauli around the nudibranch (number/2.25 cm^2), (c) mean height (mm) of hydrocauli (n = 5) within a 2.25 cm^2 area around the nudibranch, and (d) the distance (cm) between the nudibranch and the closest edge of its colony.

Habitat parameters were analyzed with a MANOVA (H_0: nudibranch habitats do not differ within colonies of *Obelia geniculata*). Habitat data were ln (x + 1) and reciprocal (x + 1) transformed (Zar, 1984; Krebs, 1989) to meet the assumptions of analysis of variance.

Perisarc analysis

Five stolons and hydrocauli were isolated from the central and peripheral (outer 2 cm) portions of five colonies of *O. geniculata* and fixed overnight in Bouin's solution. After being washed in 50% ethanol, the pieces were dehydrated, stained with acid fuchsin, embedded in paraffin, and sectioned. The perisarc was stained with Lugol's solution (Lillie, 1954) according to procedures adapted from Drury and Wallington (1980). Thickness (μm) of the perisarc of stolons, hydrocauli, and theca from each area of the colony were measured with an ocular micrometer.

A two-way analysis of variance was used to compare the thickness of perisarcs from the center and the periphery of the hydroid colony. Data were log transformed to stabilize variances. A Tukey-Kramer HSD multiple comparison test was used to test comparisons of interest among structures within and between areas of the colony (Zar, 1984; Day and Quinn, 1989).

Results

Structure of the radulae

The radulae of the four nudibranch species differed statistically in the six parameters measured (Table 1). Only the radula of *Tergipes tergipes* was curved; the others had no hook. The radula is an important taxonomic character for opisthobranchs (Thompson and Brown, 1984) and varied little among the individuals of a species.

Dendronotus frondosus had a wide ($X \pm SE = 157.70 \pm 4.51$ μm), multiseriate radula with 5–9 lateral teeth flanking the rachidian tooth (Fig. 2a). The rachidian tooth (width = 39.36 ± 1.01 μm, length = 29.93 ± 1.33 μm) was triangular with 9–11 small, lateral denticles. Each lateral tooth had a single cusp and 3–5 denticles. The rake angle was wide ($58.2° \pm 2.8$) (Fig. 2b).

The uniseriate radula of *Doto coronata* was narrow (17.80 ± 0.25 μm) (Fig. 2c). The rachidian tooth was short and stubby (width = 17.73 ± 0.26 μm, length = 7.78 ± 0.36 μm) with 3–4 large lateral denticles on each side. The central denticle of the rachidian tooth was depressed, making the dorsal surface of the radula concave. The rake angle was narrow ($21.6° \pm 1.0$) (Fig. 2d).

Eubranchus exiguus had a wide (103.70 ± 3.87 μm), triseriate radula (Fig. 3a). A single lateral tooth flanked the rachidian tooth. The rachidian tooth was long and thin (width = 28.62 ± 2.80 μm, length = 22.71 ± 0.60 μm) with 3–7 large denticles on each side; it appeared rake-like. The lateral teeth were wide at their base and tapered sharply to a thin, narrow, single cusp. The rake angle was moderately wide ($36.5° \pm 1.9$) (Fig. 3b).

*Tergipes tergipes* had a narrow (34.99 ± 2.29 μm), uniseriate radula (Fig. 3c) with a short, wide rachidian tooth (width = 30.84 ± 2.19 μm, length = 19.50 ± 1.09 μm) that bore a prominent central denticle and 5–10 large, lateral denticles. The central denticle was approximately two times longer than the lateral denticles and had a nar-

Table I

*Analyses of variance of parameters of radular structure for the four species of nudibranchs (*Dendronotus frondosus, Doto coronata, Eubranchus exiguus *and* Tergipes tergipes*)*

Variable	df	F	P
ln W_R	3, 53	397.356	<0.001
ln W_r	3, 53	56.743	<0.001
ln L_r	3, 53	83.263	<0.001
Sqr(denticles)	3, 53	94.119	<0.001
Angle	3, 53	3882.190	<0.001

Model: ln W_R, ln W_r, ln L_r, sqr denticles, angle = constant + species of nudibranch. (MANOVA: Pillai Trace = 2.328, $P < 0.001$) (sqr = square root).
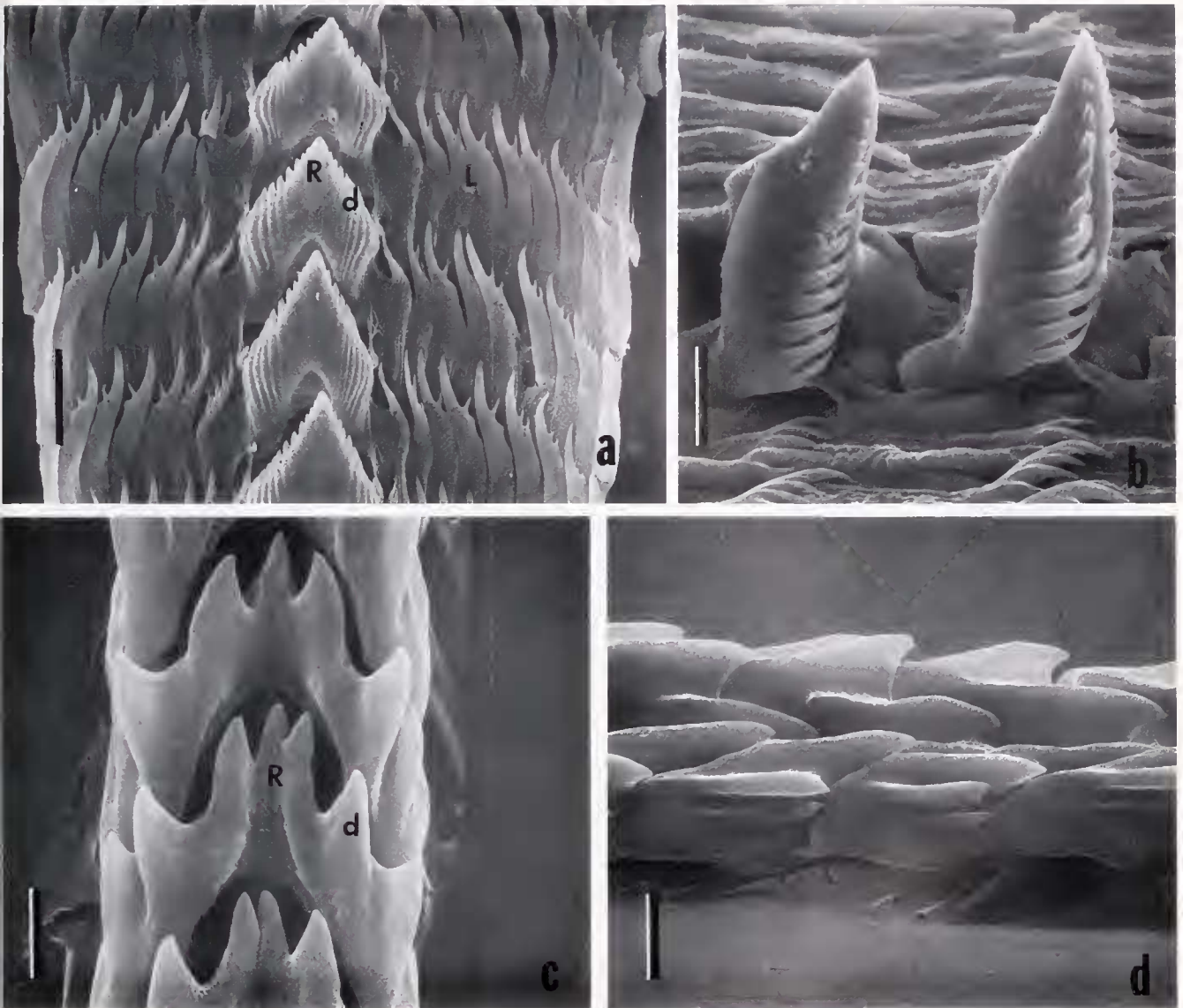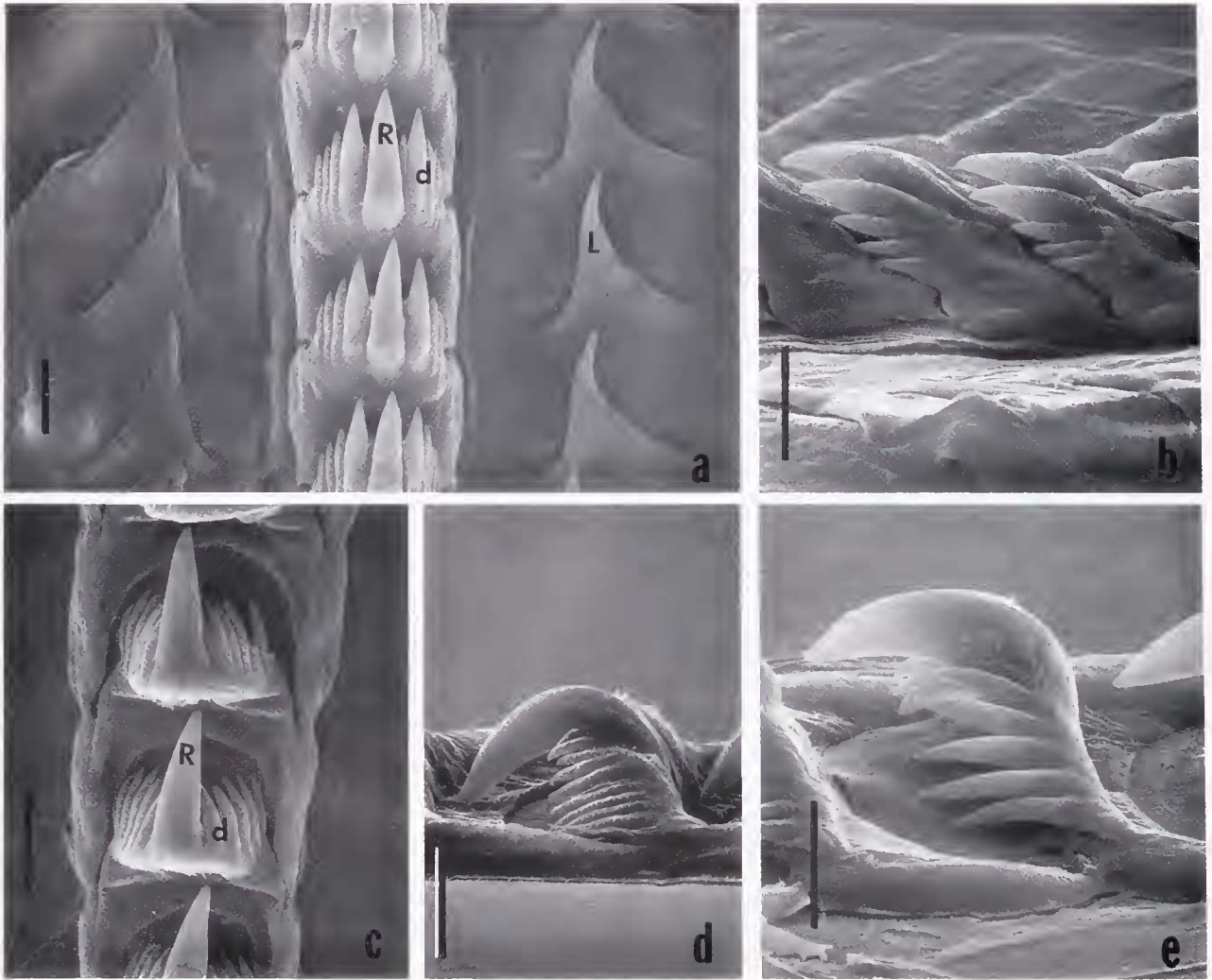
Figure 2. Scanning electron micrographs of radulae from *Dendronotus frondosus* (size = 4 mm) (a, b) and *Doto coronata* (size = 5 mm) (c, d) from a dorsal (a, c) and lateral (b, d) view. Scale bars: a = 20 μm, b = 15 μm, c, d = 5 μm. (d = denticles, L = lateral teeth, R = rachidian tooth.)

row rake angle (22.5° ± 1.9) (Fig. 3d, e). The radula of *T. tergipes* was the only one with a hook. The curvature index for all 21 tooth rows examined was 0.293, but there was considerable variation (SE = 0.04). Some of this variability could have occurred when the radulae were dried for viewing with the SEM.

Feeding behavior

Species specific behaviors for handling and consuming hydroid prey were observed in feeding nudibranchs; feeding behaviors among conspecifics varied little.

Depending upon their size, *D. frondosus* showed one of two feeding mechanisms; small individuals were suctorial feeders, whereas large individuals were polyp biters. Individuals less than 5 mm long (n = 7) penetrated the perisarc of thecae and stolons by scraping with the radula; they then grasped the hydroid with the anterior portion of their foot and sucked the tissue out. The average time required to penetrate a theca was 4.2 min (SE = 2.9). Once a hole had been made, suction created by the buccal apparatus served to draw out either the hydranth from a hydrotheca, or the juvenile medusae from a gonotheca.

Figure 3. Scanning electron micrographs of radulae from *Eubranchus exiguus* (size = 4 mm) (a, b) and *Tergipes tergipes* (size = 4 mm) (c, d, e) from a dorsal (a, c) and lateral (b, d, e) view. Scale bars: a, b, c, d = 10 μm, e = 15 μm. (d = denticles, L = lateral teeth, R = rachidian tooth.)

When feeding on gonangia, the nudibranchs plucked individual, juvenile medusae from the bottom of the gonotheca. On stolons, tissue was extracted by a few, quick pulses of the buccal apparatus.

Dendronotus frondosus individuals greater than 5 mm were polyp biters or grabbers. The nudibranchs would crawl up a hydrocaulus and lightly contact the tentacles of an exposed hydranth with the anterior portion of the foot and mouth. Both suctorial and grasping mechanisms were used to consume polyps. Although the radula was everted from the mouth, it did not contact a polyp (n = 14). As buccal activity created a suction that pulled the polyp towards the nudibranch's mouth, the jaws were protruded, and the polyp was clipped off at its base leaving only the annuli. A nudibranch would continue in this

manner along a hydrocaulus following the alternating pattern of polyp branching, feeding at a rate of 1–2 polyps per minute over a 5-min observation period (n = 6).

Doto coronata was a suctorial feeder preying predominantly on the stolons of *Obelia geniculata*. The nudibranch clutched a stolon with the anterior portion of the foot to bring the mouth against the stolon. The anterior portion of the foot flattened against the stolon during buccal activity, suggesting that the nudibranch was exerting additional pressure to assist in penetration. When a hole was produced through the perisarc, coenosarc was drawn into the animal's mouth. Tissue moved unidirectionally toward the mouth of the nudibranch in pulses that coincided with pulses of the buccal apparatus. Perisarc was penetrated by rasping with the radula. Drill holes

produced by *D. coronata* of 4–5 mm were round, with a diameter of 35.7 μm (SE = 4.8) (Fig. 4). The holes had beveled sides with grooves corresponding to the denticles of the rachidian tooth. A raised lip around the perimeter of the holes was distinct from the perisarc and is either coenosarc of the hydroid or mucous produced by glands in the foot of the nudibranch. Incomplete holes (Fig. 4c, d) had a jagged or deteriorated perisarc at their center.

The time to penetrate a stolon by *D. coronata* was difficult to determine. A hole was considered complete when the coenosarc was drawn toward the nudibranch. It was common for an individual nudibranch to position itself atop a portion of stolon for 4–6 h. During any single hour, several periods of buccal activity alternated with longer periods of apparent inactivity. The periods of buccal activity were short, usually 1–3 min with up to 15 min between sets of buccal pulses. Penetration took a minimum of 1 h, but averaged 3.3 h (SE = 1.2, n = 6).

Eubranchus exiguus was also a suctorial feeder, but fed only through the perisarc of hydrothecae. Nudibranchs grasped the base of a theca with the anterior portion of the foot, thus bringing their mouths against the perisarc. The radula scraped the thecal surface creating a hole in 15–30 s, and the entire hydranth was drawn out through the base. The nudibranch left when all tissue was removed. Penetration and consumption of the first polyp took 1–2 min (SE = 10.6 s), but each successive polyp eaten took longer to consume.

The penetration hole produced by *E. exiguus* was elliptical (Fig. 5). The sides of the holes were jagged and the perisarc appeared ripped, rather than worn or scraped as in holes in stolons produced by *D. coronata* (Fig. 4). The width of the hole at its center and widest point (X $\pm$ SE = 8.00 $\pm$ 1.07 μm) was similar to the width of the top three denticles on the rachidian tooth (6.46 $\pm$ 0.48 μm). The lateral teeth on radulae of *E. exiguus* were not observed contacting the thecal perisarc during the feeding process.

Tergipes tergipes did not penetrate the perisarc, but attacked naked tissue. Small individuals (<4 mm) placed their mouths atop a polyp and rasped tissue directly from the area around the hypostome. If the hydranth was re-
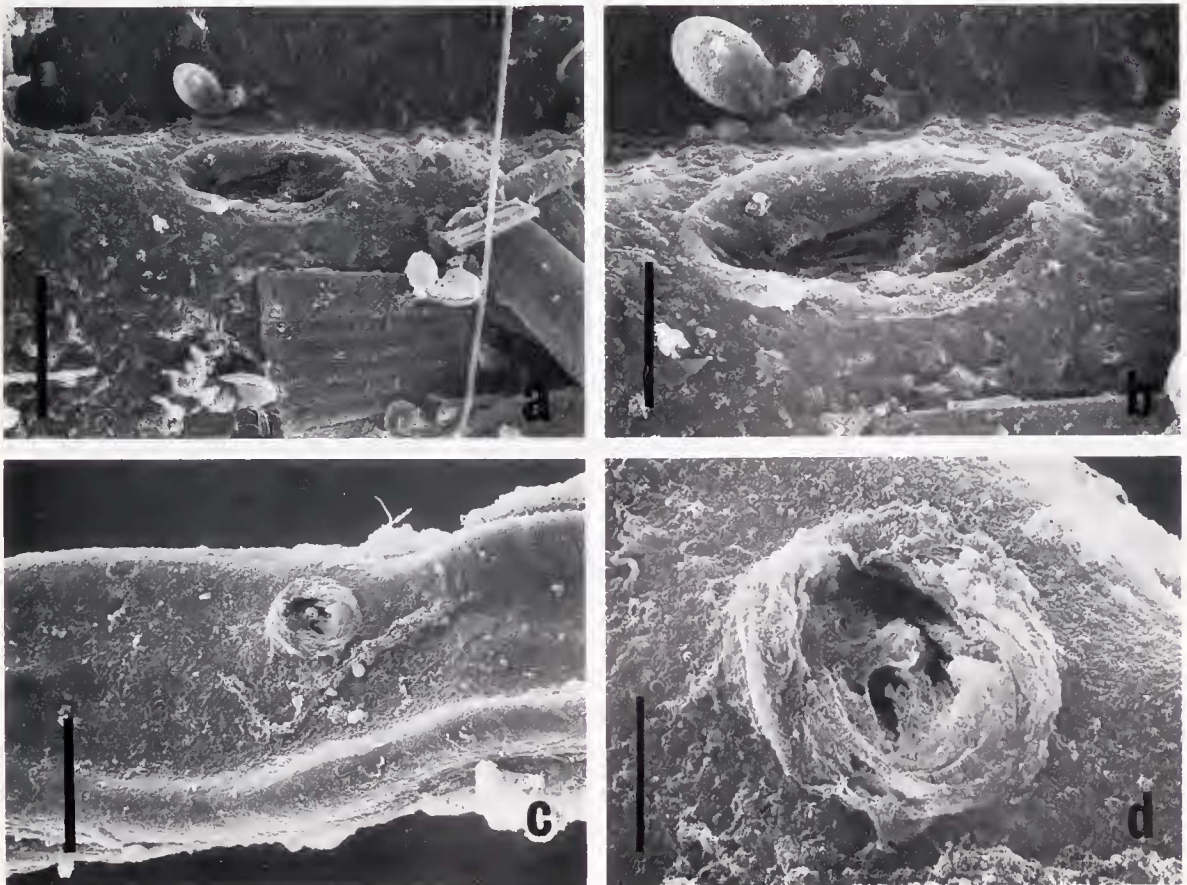
Figure 4. Scanning electron micrographs of stolons of *Obelia geniculata* showing drill holes produced by *Doto coronata* during feeding. Scale bars: a, c = 50 μm, b, d = 20 μm.
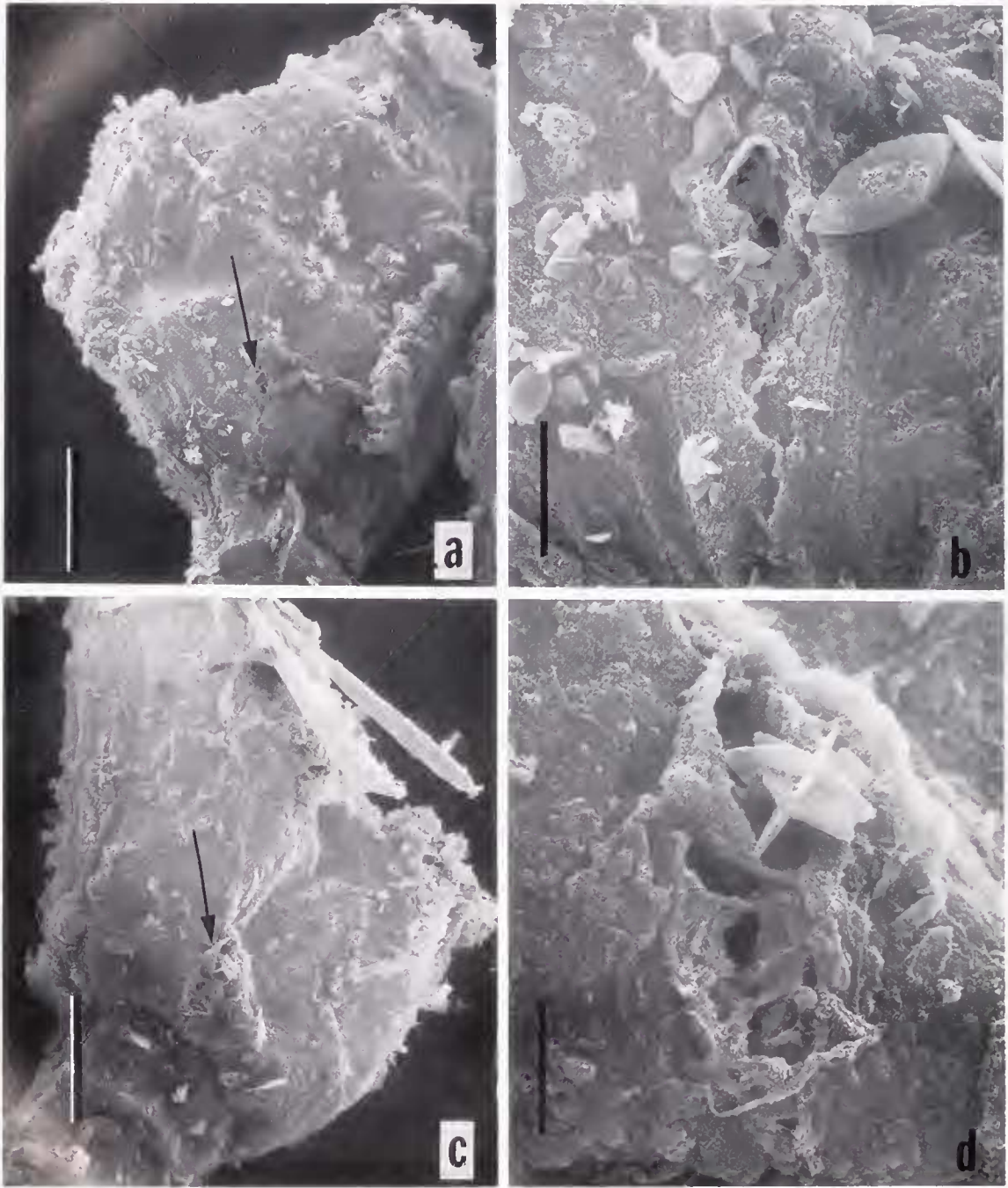
Figure 5.   Scanning electron micrographs of hydrothecae of *Obelia geniculata* showing penetration holes produced by *Eubranchus exiguus* during feeding. In a and c the arrow points to the area of damage; b, d are magnifications of these areas. Scale bars: a, c = 50 μm, b, d = 10 μm.

tracted into the theca, the nudibranch curled its body over the thecal rim to reach the polyp tissue. Very small individuals (<1 mm) crawled into hydrothecae to feed upon polyps. While direct observations clarified the use of the radula in raking tissue from the polyp, it was not determined whether the jaws were also used. Small individuals

(n = 5) of *T. tergipes* required up to 2 h to consume an entire polyp (75 ± 45 min).

Larger individuals (>3 mm) of *T. tergipes* (n = 8) either ripped the entire polyp from a hydrotheca or cropped tentacles. Each process was very rapid compared to the slow rasping of smaller *T. tergipes*. The approach to a

Table II

Analysis of variance table testing the relationship between habitat parameters of nudibranchs in colonies of Obelia geniculata *and species of nudibranch (MANOVA: Pillai Trace = 0.510, P < 0.001)*

Variable	df	F	P
Inverse height	3, 358	51.983	<0.001
Mean height	3, 358	11.115	<0.001
ln density	3, 358	8.827	<0.001
ln distance from edge	3, 358	13.981	<0.001

Model: Inverse (height on an hydrocaulus + 1), Mean height of hydrocauli, ln (density of hydrocauli around a nudibranch + 1), ln (distance from the edge of the colony + 1) = constant + species.

polyp, consumption of the polyp, and departure from the branch took as little as 60 s (150 ± 75 s), and one individual ate 60–80% of a whorl of tentacles on a polyp in 25–30 s.

Habitats of nudibranchs

Sizes of *D. frondosus*, *D. coronata*, and *E. exiguus* were not significantly related to the four habitat parameters measured. However, height and density of hydrocauli around a nudibranch were related to size of *T. tergipes* ($P < 0.001$, $P = 0.10$, respectively). Large nudibranchs of *T. tergipes* were in areas with taller, more numerous hydrocauli.

Each nudibranch species occupied a particular area within the hydroid colony. Each of the four habitat parameters measured was important in distinguishing where a particular nudibranch species occurred in a hydroid colony (Table II). A Tukey-Kramer HSD test was performed to determine differences between species within each habitat parameter (Table III).

Nudibranch species occupied different heights on hydrocauli (Table III). *T. tergipes* was consistently on hydrocauli well above the bottom of the hydroid colony and was seen crawling at the bottom of the colony in only 6% of all observations (n = 193). It also positioned itself higher on hydrocauli (6.0 ± 0.3 mm) than *D. frondosus* and *D. coronata* ($P < 0.001$), but its position was not significantly different from *E. exiguus* (5.6 ± 0.1 mm). *E. exiguus* was on hydrocauli 69% (n = 16) of the time and its position differed from *D. frondosus* and *D. coronata* ($P < 0.001$). *D. frondosus* maintained an intermediate position within the vertical component of the colony with individuals 3.0 mm (SE = 0.5) above the kelp surface, but in 56% (n = 77) of the observations *D. frondosus* was on stolons or crawling on the kelp surface. *D. coronata* was at the bottom of the colony on stolons or on the kelp surface (0.6 ± 0.3 mm) in 90% (n = 76) of all observations.

Mean height and density of hydrocauli were quantified to describe the immediate area (2.25 cm²) around each species of nudibranch. The hydrocauli around *D. frondosus* (15.7 ± 0.6 mm) were significantly taller than those around all other nudibranchs ($P < 0.001$). The height of hydrocauli around *T. tergipes* (13.3 ± 0.3 mm), *E. exiguus* (12.3 ± 0.3 mm) and *D. coronata* (11. ± 0.5) were not significantly different from each other (Table III). The density of hydrocauli around individuals of each species of nudibranch showed the same general pattern (Table III). The areas around *D. frondosus* (14.6 ± 0.6 hydrocauli/2.25 cm²) and *T. tergipes* (13.4 ± 0.5 hydrocauli/2.25 cm²) contained a similar and higher density of hydrocauli and both were significantly different ($P < 0.001$) from the areas around *E. exiguus* (10.7 ± 0.4 hydrocauli/2.25 cm²) and *D. coronata* (10.3 ± 0.5 hydrocauli/2.25 cm²). *E. exiguus* and *D. coronata* occupied areas that were not significantly different from each other.

T. tergipes tended to occupy a more central area of the colony. Nudibranchs were 4.05 cm (SE = 0.2) from the edge of the colony. *T. tergipes* was further from the edge of the colony than *D. coronata* and *E. exiguus* ($P < 0.001$), but not significantly different from *D. frondosus*. *D. frondosus* was 2.65 cm (SE = 0.2) from the edge of the colony. *D. coronata* and *E. exiguus* occupied similar areas of the

Table III

Summary of habitats of nudibranchs inhabiting colonies of Obelia geniculata. *Vertical lines within a habitat parameter indicate significant differences (Tukey's, P < 0.05) between species of nudibranchs for each parameter*

	Height on upright	Height of uprights around nudibranch	Density of uprights around nudibranch	Distance from edge of colony
High	Tergipes Eubranchus	Dendronotus	Dendronotus Tergipes	Tergipes
Mid	Dendronotus	Tergipes Eubranchus	Eubranchus	Dendronotus
Low	Doto	Doto	Doto	Doto Eubranchus

colony as *D. frondosus* (Table III). *D. coronata* was 2.62 cm (SE = 0.2) from the edge of the colony while *E. exiguus* was 2.28 cm (SE = 0.3) from the edge of the colony.

Perisarc analysis

The thickness of the perisarc of colonies of *O. geniculata* differed among structures (stolons, hydrocauli, thecae) within an area of the hydroid colony (F = 186.73, *P* < 0.001) (Fig. 6). Along the edge of the colony, the thickness of perisarcs of each structure differed, while in the center of the colony the perisarcs surrounding stolons and hydrocauli were similar, but both were significantly thicker than the perisarc covering the hydrothecae. Between areas of the hydroid colony, the perisarcs surrounding stolons and hydrocauli were thicker in the center than at the edge of the colony (*P* < 0.001), while they were not significantly different on hydrocauli.

Discussion

Radular structures, feeding mechanisms and micro-habitats vary in nudibranchs co-occurring within colonies of *Obelia geniculata*. Each nudibranch species used a distinct method to ingest hydroid tissue; little overlap existed between species. Individuals within a species showed some variation with respect to the hydroid structure they fed upon, but small nudibranchs (<6 mm) appeared to be restricted mostly by the structure of their radula (Hinde, 1958; Nybakken, 1970; Mills, 1977). Nudibranchs occupy areas of *O. geniculata* colonies in which they can feed, suggesting that feeding biology dictates habitat use for this suite of nudibranchs.

Feeding biology

Nybakken and McDonald (1981) predicted that nudibranchs with wide, triseriate radulae should feed upon naked hydranths and gonophores. *Dendronotus frondosus* has a wide, multiseriate radula (Fig. 2a), and Robilliard (1970) described the general feeding behavior of *D. frondosus* as biting whole polyps and sucking coenosarc. My findings support Robilliard, but I found that the mechanisms used by *D. frondosus* changed from piercing and sucking to biting with increase in size. Christensen (1977) described a mechanism of coordinating jaws and radula for feeding by *Precuthona peachi* on *Hydractinia echinata* similar to that for *D. frondosus*. Because *P. peachi* has a uniseriate radula (Thompson and Brown, 1984) in contrast to *D. frondosus*, nudibranch size relative to hydroid prey may be a better indicator of feeding mode than is radular structure.

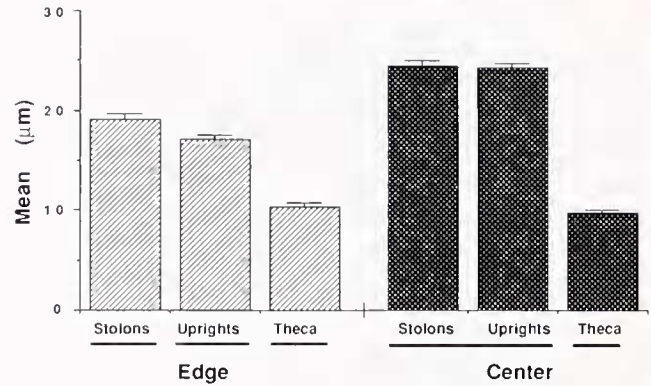*Eubranchus exiguus* with a triseriate radula penetrated the base of hydrothecae, contrary to the predictions of

Figure 6. Mean thickness (±SE) of the perisarc of *Obelia geniculata* from stolons, hydrocauli, and thecae from central and peripheral areas of the hydroid colony. Horizontal lines indicate significant differences (*P* < 0.001) for structures within an area of the hydroid colony.

Nybakken and McDonald (1981). The jaws may assist penetration of a hydrotheca by pinching the thin perisarc. The lateral teeth are very thin, delicate structures that may have little functional utility and may be vestigial. The Eubranchidae are one of only two families within the superfamily Acleioprocta that have retained a triseriate radula (Schmekel and Portmann, 1982) and Schmekel (1985) suggested that a reduction from broad radulae to narrow radulae has occurred in the evolution of opisthobranch radulae. Two mechanisms for removing tissue after penetrating the hydrotheca are feasible: (1) the rachidian tooth pulls the polyp out from the bottom of the cup or (2) the buccal apparatus assists by creating a vacuum for suction (Kohn, 1983). The second mechanism is more probable because polyps are rapidly extracted through the base of a theca rather than incrementally drawn out as would occur if rasped.

According to Nybakken and McDonald (1981), nudibranchs with uniseriate radulae should feed upon stolons that are covered with perisarc. They suggested that a uniseriate radula is better adapted for drilling holes than radulae with three teeth per row, but *Doto coronata* and *Tergipes tergipes* both have narrow, uniseriate radulae. *D. coronata* feeds by rasping a hole through stolons, whereas *T. tergipes* rakes naked tissue of hydranths.

The radula of *D. coronata* is flat with the central denticle of the rachidian tooth depressed below the lateral denticles (Fig. 2c, d). The penetration holes are circular (Fig. 4) and similar to those produced by muricid snails (Carriker, 1969), octopods (Nixon and Maconnachie, 1988) and by the dorid nudibranch *Okadaia elegans* (Young, 1969). Each of these predators preys upon organisms that have a calcareous exoskeleton (mollusks) or live in calcareous tubes (serpulid polychaetes) and use chemicals to assist the penetration process. Muricid and naticid snails use

secretions from an accessory boring organ (Carriker, 1969, 1981), octopods use saliva from the posterior salivary glands (Nixon, 1979a, b; Nixon and Maconnachie, 1988) and Young (1969) suggests that *O. elegans* uses secretions from glandular cells around the lumen of the mouth, which he considers are part of the stomodeal gland. The etched pattern along the sides as well as the deteriorated top of the penetration hole produced by *D. coronata* suggest the presence of a caustic agent (Fig. 4b, d). The behavior of *D. coronata*, which sits atop stolons for long periods of time with short pulses of the buccal apparatus alternating with longer periods of inactivity, is similar to the drilling-related behavior of the snail *Urosalpinx* (Carriker, 1969), and suggests *D. coronata* may use chemicals to assist in the penetration of chitinous perisarc of *O. geniculata*. No reports show that dotoids possess glands capable of secreting substances for dissolution of prey skeleton. The salivary glands are unlikely candidates because they do not produce secretions containing lytic enzymes (Hyman, 1967; Welsch and Storch, 1973); however, histochemical work is needed to elucidate this mechanism.

Nybakken and Eastman (1977) showed that the curved radula of *Triopha carpenteri* is better for ripping flesh from erect bryozoa than the flat radula of *Triopha maculata*, which is used to scoop polypides from colonies of *Membranipora membranacea*, an encrusting bryozoan. The feeding mechanism observed for *T. tergipes* with a narrow, hooked radula is similar to the mechanism used by *T. carpenteri*. Feeding on polyp tentacles by slurping seems to be restricted to larger individuals (>3 mm) and may be a function of mouth size and ability to engulf whole strands of tissue.

Size

The nudibranchs inhabiting colonies of *Obelia geniculata* are all very small; nudibranchs greater than 5 mm are seldom found (Lambert, 1991). The mechanism each species uses to feed may in part be dictated by its size, in addition to the structure of its radula. Heavy jaws are used to break through relatively thin exoskeletons encasing zooecia of ectoproct colonies by the large dorids *Triopha carpenteri* and *T. maculata* (Nybakken and Eastman, 1977). *D. frondosus* may grow to 100 mm (Thompson and Brown, 1984), and animals larger than 5 mm use jaws to bite off whole polyps, a feeding mechanism similar to *Triopha* spp.

Newly metamorphosed juveniles may experience constraints due to size (Todd, 1991) when feeding upon *O. geniculata*. Because three of the four nudibranchs in colonies of *O. geniculata* feed by penetrating perisarc at some point during post-larval life, do any of these require an intermediate diet? *O. geniculata* may be considered an intermediate diet for juvenile *D. frondosus* because adults feed on larger tubularian hydroids. Both *D. coronata* and *E. exiguus* feed by penetrating the perisarc, but it is more likely that *D. coronata* is constrained by prey size because it feeds through the thicker stolon perisarc. Because long periods of time (2–4 h) are required for an adult *D. coronata* to penetrate a stolon, one could hypothesize that meiofaunal-sized juveniles are unable to efficiently drill through stolons. A microalgal diet would allow tiny nudibranchs to increase size before shifting to the adult prey. *T. tergipes* feeds on naked polyp tissue and is not constrained by its size; newly settled nudibranchs crawl into hydrothecae and rasp tissue directly (Lambert, 1990).

Habitats and feeding

Distribution within the hydroid colony and on hydrocauli demonstrated that nudibranchs segregate to areas in which they can feed. *D. frondosus* is a generalist predator within colonies of *O. geniculata*. Nudibranchs greater than 12 mm infrequently occupy colonies of *O. geniculata* (Lambert, 1991) and associate among athecate hydroids, particularly *Tubularia* spp. (Swennen, 1961; Thompson, 1964; Robilliard, 1970; Clark, 1975; Todd, 1981). Because large *D. frondosus* are very obvious in colonies of *O. geniculata* (pers. obs.), shifting to *Tubularia* colonies may provide a better refuge from fish predation as well as necessary calories.

Doto coronata occupied the edge of colonies, at the bases of hydrocauli or on the kelp surface and among few, short hydrocauli and fed predominantly on stolons. The perisarc of stolons is thinner along the perimeter of colonies than at the center and appears to be selected as a prey that is easier to handle (Pyke *et al.*, 1977). The preference to feed at the growing edge of colonies is similar to that in dorid nudibranchs, which feed at the edges of bryozoan colonies (Harvell, 1984; Todd and Havenhand, 1989). This behavior in dorids has been related to the lower calcification and strength of edge zooids (Best and Winston, 1984) and to differences in palatability of structures between zooids in a colony. Harvell (1984) suggested that colonies of *Dendrobeania lichenoides* have an ontogenetic gradient marked by morphological and physiological variation in tissue content of zooids. The gradient affects the grazing patterns of nudibranchs, which prefer to feed upon zooids at the perimeter, that are free of brown bodies and reproductive structures. In the case of *D. coronata*, the preference for stolons along the perimeter of colonies seems to be due to a greater mechanical ease of penetration. Composition of the coenosarc differs between the growing edge and the center of colonies of *O. geniculata* with respect to cellular activity (Crowell, 1957; Braverman, 1971), but no reports discuss differences in

nutritional value between areas in hydroid colonies as were found in bryozoan colonies (Harvell, 1984).

Eubranchus exiguus was usually high on hydrocauli in areas where they were relatively numerous and tall. *E. exiguus* fed by penetrating hydrothecae and suctioning tissue and is thus found where the hydrothecae have the thinnest perisarc coverings (Fig. 6) and are more numerous (Crowell, 1957).

Tergipes tergipes feeds on exposed polyps and is found where food is most abundant, among many, relatively tall hydrocauli in the center of the colony. Crowell (1957) and Braverman (1963) showed that the centers of hydroid colonies are taller, denser, and have more polyps than the periphery.

Coexistence

The four species of nudibranchs found in colonies of *O. geniculata* differed in radular morphology, feeding behavior and micro-habitat. Thus, factors preventing competitive exclusion exist and traditional equilibrial coexistence could have operated (Connell, 1980), but large fluctuations and temporal shifts in abundances of populations are sufficient to explain species co-occurrences without competition (Birch, 1979; Chesson and Case, 1986; Hajek and Dahlsten, 1986). Relative abundances and age distributions of each population of nudibranch in the present study are temporally mediated (Lambert, 1991), and alternative food resources and habitats are present during the summer when nudibranch populations are highest (Lambert, 1985, 1991; Kuzirian, unpub. data). Also, because the majority of nudibranch larvae recruit to benthic habitats by the settlement of passively dispersed larvae (Todd, 1981), pre-settlement mortality could greatly contribute to variation in recruitment (Mileikovsky, 1974; Young and Chia, 1987). Thus, the apparent lack of a limiting resource and the absence of equilibrial population levels suggest that competition is unimportant among these nudibranchs (see Wiens, 1977; Strong *et al.*, 1984).

Behavioral interactions among organisms in a community can influence the use of resources by the species (Race, 1982; Brenchley and Carlton, 1983). Interspecific encounters among nudibranchs in *O. geniculata* occur frequently, but they do not influence the location of nudibranchs within the hydroid colony or where the nudibranchs feed (Lambert, 1990). These nudibranchs generally appear indifferent to the presence of others. Intraspecific encounters between pairs of nudibranchs result in non-aggressive responses (Lambert, 1990). The behavioral patterns of this assemblage of nudibranchs appear similar to some populations of phytophagous insects (Root, 1973; Simberloff, 1978; Strong, 1982; Hajek and Dahlsten, 1986), where non-equilibrial processes structure the community (Strong *et al.*, 1984).

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